USDA Forest Service
Research Paper INT-144
1973

POSSIBILITIES FOR IMPROVEMENT OF WESTERN WHITE PINE BY INBREEDING

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Cover Photo.--Growth differences are evident between this 20-year-old S_1 tree (63 X 63) No. 3 (left) and one of its 20-year-old half-sibs (63 X 62) No. 2 (right), at the Moscow Arboretum, December 1972.

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ABSTRACT

Pinus monticola S_1 seedling mortality, timing and extent of fruiting, strobilus attrition, crossing success, seed yield, and seed weight are compared for 18 S_1 lines and their outcrossed half-sib lines. No reproductive barriers are restrictive enough to preclude continued inbreeding. Filled seed yields from second generation inbreeding are low but consistent and large enough to justify continuing an experimental program. Results of experimental single crossing between S_1 lines should guide decision on a practical inbreeding program.

INTRODUCTION

Investigations of the effects of inbreeding in western white pine (*Pinus monticola* Dougl.) have been underway at this Station since 1950 (Bingham and Squillace 1955). Over 150 S_1 seedling lines have been developed, each usually produced along with four full-sib outcrossed seedling lines of the same mother tree (i.e., half-sibs of the S_1's). S_1's and their outcrossed half-sib seedlings (hereafter called half-sibs) have been artificially inoculated with the white pine blister rust fungus (*Cronartium ribicola* J. C. Fisch. ex Rabenh.), and seedlings that survived the rust exposure (ranging from 0 to 20 S_1's and 5 to 30 half-sibs) have been established in a blister rust resistance arboretum at Moscow, Idaho.[1] The oldest of these resistant seedlings are now 21 years of age. There has been substantial fruiting of the half-sib seedlings for about 10 years, but only sporadic fruiting of the S_1 seedlings for about 5 years, with the first substantial fruiting in 1972.

Blister-rust-inoculated S_1 seedling lines have been of immediate value for supporting hypotheses on the presence of recessive resistance genes in western white pine (McDonald and Hoff 1971). Now that the S_1 lines are reaching reproductive maturity, however, they are becoming useful for assessing possibilities and limitations of classical inbreeding methods (Shull 1910; Jones and Singleton 1935) for improvement of growth and other traits.

This paper considers the feasibility of an inbreeding program in western white pine, its likely timing and promise. Data presented here are mainly restricted to cone and seed bearing following controlled crossings on 18- to 21-year-old S_1 trees in 18 different lines. Second-generation inbred cone yields and seed progenies discussed include those from selfing S_1 trees (S_2 crosses), S_1 full-sib crosses, S_1 backcrosses, single crosses (between unrelated S_1's), and other inbred crosses of the second and first generation. Descriptions and examples of these inbreds are given in "Materials and Methods," starting on page 5.

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[1]Progress reports on breeding for blister rust resistance in western white pine include Bingham and others 1953, 1960, 1969, and 1972.

LITERATURE REVIEW

An extensive literature deals with effects of first-generation selfing in conifers, especially *Pinus*. The summary by Franklin (1970) covers much of this literature through 1967, and adequately describes effects of inbreeding as reflected in S_1 cone and seed yields, seed germination, and mortality and early growth of S_1 seedlings. His table 3 sums up these S_1 effects in *Pinus*, pointing out that in general, and in comparison to outcrossing, neither cone yield nor total (filled plus hollow) seed yield are affected, filled seed yield is reduced about one-third, hollow seed yield is increased about 2-1/2 times, seed germination is reduced about one-tenth, seed weight is little affected, seedling mortality is about one-third higher, and seedling height is reduced about one-fourth.

These general conclusions are quite applicable to western white pine, except that in young trees (18 to 21 years) cone yield may be reduced, if not in the older trees (30 to 50 years) covered by Franklin.

Several times in the past (Bingham and Squillace 1955; Squillace and Bingham 1958; Barnes and others 1962) we have noted the wide variation in self-fertility of different western white pine mother trees. Some trees are comparatively self-fertile, others self-sterile, in respect to seed yield, as is shown in table 1. The self-fertile trees like parent 58 are equal or better in filled S_1 seed yield and give somewhat greater hollow seed yield. The seat, manner of operation, and timing of the incompatibility mechanisms are unknown, but the effect is strongly associated with the mother tree.

In contrast, literature on second-generation inbred crossing is very sparse. Only five reports of crossing of S_1 trees have been found. Some of this information was outlined by Franklin (1970), but is reviewed more completely in this paper, so that sounder conclusions may be drawn as to the feasibility of continued inbreeding or the likelihood of improvement of conifers by use of classical inbreeding methods.

Table 1.--*Seed yield, seed weight, and seedling emergence, for a comparatively self-fertile and a comparatively self-sterile western white pine tree*[1]

Polli-nation year	Type of cross	Number of crosses	Filled seed per cone[2]	Hollow seed per cone[2]	Seed weight[2]	Seedling emergence[2] [3]
					Mg.	*Percent*
			SELF-FERTILE TREE 58			
1950	Self	1	134			84
	Outcross	11	106			87
1954	Self	1	88	44	18.1	52
	Outcross	2	68	36	17.4	42
1957	Self	1	103	20	18.2	
	Outcross	1	121	4	19.1	
All years	Selfs	3	108			
	Average outcrosses	14	98			
			SELF-STERILE TREE 19			
1950	Self	1	24			83
	Outcross	18	35			84
1954	Self	1	31	63	22.4	58
	Outcross	1	61	14	22.1	64
All years	Selfs	2	28			
	Average outcrosses	19	49			

[1]Data from Bingham and Squillace (1955), Squillace and Bingham (1958), and Barnes and others (1962).

[2]Results for groups of outcrosses are average values.

[3]Emergence of seedlings in the nursery seedbeds is probably less than their total germination.

The oldest material reported upon in the literature concerns five 55-year-old Norway spruce (*Picea abies* (L.) Karst.) S_1 trees in two S_1 lines developed by Swedish silviculturist Nils Sylven through self-pollinations made in 1909! Langlet (1940), and later Eriksson and others (1973) reported upon inbreeding effects in this very old material. Andersson (1965) selfed the five S_1 trees. Four of the S_1's produced cones, three produced filled S_2 seeds. Cone and S_2 seed yields are given in "Discussion," starting on page 12, where they are compared with those of three other conifers, including western white pine. About one-half, or 21, of the filled S_2 seed in three different S_2 seed lots germinated in a Jacobsen germinator, but no information is given on their subsequent survival and growth. Andersson noted that a greater reduction in germination occurred between outcrosses and S_1 seed than between the S_1 and S_2 seed.

Dr. Wolfgang Langner produced S_1's of Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Gord.) in Germany from self-pollinations made in 1936. Later, Langner (1961) reported upon second-year height of S_2's coming from these S_1's, and on related progenies, as shown below.

	Outcrosses	*Half-sibs*	*Full-sibs*	*S_2's*
Inbreeding coefficient (F)	0.000	0.125	0.250	[2]0.750
Average height (cm)	37.3	32.7	29.7	24.7

Just a few years later in 1938 and 1941, Dr. C. Syrach Larsen also selfed Japanese larch, as well as European larch (*Larix decidua* Mill.). Later, Keiding (1962) crossed the Japanese and European larch S_1's, noting that the single cross interspecies hybrids produced outgrew the parents. Effects of inbreeding within species could not be separated, however, from effects of interspecies hybridization: Keiding stated, "It was not possible to prove any additional effects of inbreeding and outcrossing."

The next oldest material is that of Orr-Ewing (1954, 1965, 1969). Self-pollinations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) parental trees were begun in 1952, and continued through 1968. Within 8 to 10 years about one-third of the S_1 trees in seven out of eight S_1 families (1 to 98 trees per line) were producing an average of 10 to 14 female strobili per tree (Orr-Ewing 1965). In the same time, S_1's in only three of the eight families produced male strobili. Amounts of pollen ranged from inadequate for a single pollination to enough for four or more pollinations. Outcrossed sibs of the same parent trees had almost twice as many sporophylls per male strobilus, but pollens of S_1's or outcrossed sibs were indistinguishable. Orr-Ewing (1965) went on to show that on the average about half of the filled S_2 seed germinated (here in eight S_2 lines), and finally, that the average first-year height of S_2 seedlings in six lines varied between 27 and 59 mm. Many S_1 backcrosses, S_1 sib crosses, and two single crosses were also reported upon. Cone and seed yields of the S_2 and these crosses also are given in "Discussion," starting on page 12. Orr-Ewing (1969) reinforced his earlier finding of variability in average height of 1-year-old S_2 seedling families (range 79 to 158 mm). His general conclusions (Orr-Ewing 1954, 1965, 1969) were that in Douglas-fir, inbreeding would be sufficiently rapid and easy to be entirely feasible, and that variation in inbreds was great enough so that an inbreeding program probably would be rewarding. Some of the single-cross progenies looked quite promising, and selection among S_1's would have had pronounced effects on single cross seedlings. Unfortunately, no control (outcrossed) seedlings were compared with the single cross seedlings.

The youngest material reported upon is that of Katsuta (1966), who began selfing Japanese black pine (*Pinus thunbergiana* Franco) and the Japanese red pine (*Pinus densiflora* Sieb. and Zucc.) in 1956. Within 7 to 8 years, S_1 trees of Japanese black pine were fruiting so that S_2's and S_1 sib crosses, S_1 backcrosses, and single crosses could be attempted. Cone and seed yield from these second-generation inbred crossings also are given in "Discussion," starting on page 12. Apparently second-generation inbred seeds were not sown. Katsuta remarked that S_2 seed yields were "considerably high."

Useful comparisons have been made of the association of certain characteristics with increasing inbreeding coefficient F. Langner (1961) showed a decrease of about 5 percent in height of 2-year-old Japanese larches, and Squillace and Kraus (1962) showed decreases of five seed per cone and 8 percent in germination in 1-year-old slash pine (*Pinus elliottii* var. *elliottii* Engelm.), for each 0.1 increase in F.

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[2]Given by Langner as 0.625.

MATERIALS AND METHODS

Between 1950 and 1970, first-generation selfings were attempted on about 200 western white pines in natural stands of northern Idaho. Seed and S_1 seedling lines were produced from more than 150 of these selfs, but seedlings of only about 50 S_1 lines remained after blister rust resistance testing. The resistant S_1 seedlings were transplanted into the blister rust resistance arboretum, where in 1972 they ranged from 8 to 21 years of age. The trees below age 18 so far have fruited very infrequently, however. Therefore, only 109 S_1 trees in the 18- to 21-year-old age bracket, one to 18 trees in each of 22 S_1 lines, constitute the inbred materials covered in this paper. At present only 72 of these S_1's in 18 different lines survive. Some S_1's in 17 of the 18 surviving S_1 lines have fruited. Outcrossed materials for comparison consist of over 1,000 surviving trees in 158 lines. All outcrossed trees are half-sibs of the S_1 trees, and of the same ages. These half-sib trees occur in 140 full-sib and 18 wind-pollinated progenies of the same 22 mother trees, and there are from 4 to 235 trees in each of the 22 mother-tree lines.

Female strobilus production on S_1's began in 1960, when single 9-year-old S_1 trees of two lines produced one or two strobili. Although pollinated, none of the three strobili developed beyond that juvenile stage. The first mature cones and filled seeds on S_1 trees were produced on 11-year-old S_1's in 1962, from 1961 pollinations. Male strobilus production on S_1's was delayed until 1966, and then occurred only on a single 13-year-old tree. By 1972, however, some S_1 lines were producing large volumes of pollen (up to 35,000 male strobili), and one S_1 line had produced male strobili every spring for 6 years. Complete records on both female and male strobilus production were maintained on all trees in the arboretum through 1966. Thereafter, because female fruiting became so general and abundant, only male strobilus counts were continued.

Over the 13 years since female strobilus production commenced on S_1 trees, many kinds of inbred matings have been attempted on the S_1's or on their half-sibs. Before S_1 pollens became available, the S_1's that bore female strobili were backcrossed to their natural-stand parents or outcrossed to other natural-stand parents, using stored pollens. Then, as the related but outcrossed half-sibs began producing pollen, the S_1's were mated with these in half-sib crosses, or the related half-sibs were themselves crossed in half- and full-sib, backcross, self, or outcross matings. Finally, and mainly in the last 5 years after S_1 male strobilus production attained substantial proportions, S_2 crosses, S_1 full-sib crosses, S_1 backcrosses, and single crosses between S_1's of two different lines were attempted. Thus, cone and seed yields from inbreds representing a range of levels of inbreeding ($F = 0.125$ to 0.750) can be compared. These inbred yields can also be compared with those from the outcross population of 158 related half-sibs.

The various first- and second-generation inbred crosses compared may be more clearly understood from examples of their pedigrees (table 2). In calculating the inbreeding coefficients, original parents were assumed not to be inbred.

Table 2.--*Types of crosses and examples of pedigrees of western white pine trees supplying study data*

Type of cross	Number of crosses attempted	Arboretum female parent: F_1 or S_1 line Female : Male	Arboretum female parent: Sibling number		Arboretum male parent: F_1 or S_1 line Female : Male	Arboretum male parent: Sibling number	Inbreeding coefficient (F)
Population outcross	642	(19 x 1)		X	(58 x 17)		[1]0.000+
Half-sib cross	35	(19 x 1)		X	(58 x 19)		0.125
Full-sib cross	87	(19 x 1	- 1)	X	(19 x 1	- 2)	0.250
First generation backcross	134	(19 x 1)		X	19 (original parent)		0.250
S_1 X outcross	4	(19 x 19)		X	(58 x 17) or x 58 (original parent)		0.000
S_1 single cross (crossing of unrelated S_1's)	67	(19 x 19)		X	(58 x 58)		0.000
S_1 X half-sib	3	(19 x 19)		X	(19 x 58)		0.250
S_1 cross (selfing of an F_1)	46	(19 x 58	- 1)	X	(19 x 58	- 1)	0.500
S_1 backcross	60	(19 x 19)		X	19 (original parent)		0.500
S_1 X full-sib	22	(19 x 19	- 1)	X	(19 x 19	- 2)	0.500
S_1 X self (S_2 cross)	9	(19 x 19	- 1)	X	(19 x 19	- 1)	0.750

[1]Degree of inbreeding in natural populations is unknown, but the coefficient probably exceeds zero.

RESULTS

Various trees, both S_1's and outcrossed half-sibs, many represented by only a few trees per line, could be crossed only to the extent of their variable and often limited female or male fruiting. An extremely uneven mating pattern resulted, rendering many statistical analyses impractical. The only analyses attempted are estimations of the significance of the mean differences between S_1's and their related but outcrossed half-sib lines as to mortality, timing and extent of strobilus production, success of crossing, female strobilus loss, numbers of filled and hollow seeds, and seed weight (table 3). The body of data is large enough, however, to allow conclusions on the limitations and practicality of continued inbreeding in western white pine to be drawn with some confidence.

Survival of S_1 Trees

In 22 S_1 lines, a total of 109 trees survived exposure to the blister rust fungus in the nursery and were transplanted into the arboretum. Of these, 72, or 66 percent, survived in 1972, or at least had fruited prior to death (table 3). In comparison, 92 percent of the 1,014 outcrossed trees, in 140 full-sib and 18 wind-pollinated lines, all half-sib to one or the other of the S_1 lines, survived or had fruited. More than 25 percent lower survival in S_1's was significant. Nevertheless, survival was adequate for proceeding with second-generation inbreeding. Survival seems to be somewhat higher in S_1 lines from self-fertile parents like 25 and 58.

Comparative Delay and Extent of Fruiting of S_1 Trees

Onset of fruiting, and its extent in seasons fruited, proportion of trees fruiting, and total number of strobili borne are also shown in table 3, for 18 surviving S_1 lines and their corresponding outcrossed half-sib lines. It is remarkable that bearing of female strobili by S_1's as compared with outcrosses is delayed only about 3 years, and that a higher proportion (more than 20 percent) of the S_1 trees bore female strobili. Perhaps female fruiting is under control of one or a few recessive genes, and thus is enhanced by selfing. Otherwise, all features of timing and extent of female fruiting are in favor of the outcrossed half-sibs. In the S_1 trees, male fruiting is delayed more than two, probably several, years. Female strobili are borne only two-thirds as frequently, male strobili one-fifth as frequently; over 20 percent fewer trees produce male strobili; and total strobilus counts are only one-fourth (female) to one-sixth (male) as great as in the related half-sibs.

Table 3.--*Comparison of western white pine* S_1 *trees and outcrossed trees (half-sibs of the* S_1*'s) as to tree survival, timing and extent of fruiting, attrition of female strobili, and seed production and weight*

Parent (mother) tree number (1)	Type of tree crossed[1] (2)	Different half-sib lines (3)	Trees planted/ trees surviving[2] (4)	Age of trees in 1972 (5)	Avg. age 1st female strobili borne (6)	Different years female strobili borne (7)	Avg. age 1st male strobili borne (8)	Different years male strobili borne (9)	Different trees bearing strobili: Female (10)	Different trees bearing strobili: Male (11)	Total strobili[3] borne per avg. tree all years: Female (12)	Total strobili[3] borne per avg. tree all years: Male (13)
				Years	*Years*		*Years*					
1	S_1		2/1	19	15.0	3	[5]19+	0	1	0	0	0
	half-sib	4	14/12	18,20,21	10.3	4	10.2	5	4	6	2	325
15	S_1		2/1	18	16.0	1	18+	0	1	0	0	0
	half-sib	8	38/34	18-21	10.2	7	16.6	6	20	13	7	550
17	S_1		8/2	18	14.5	6	16.6	3	2	1	0	585
	half-sib	6	74/70	18-21	10.9	10	17.6	9	42	37	7	2295
18	S_1		1/0									
	half-sib	5	22/21	18-21								
19	S_1		17/12	21	14.0	8	17.5	3	11	2	2	1
	half-sib	33	251/235	18-21	11.0	13	17.5	9	152	102	8	1100
20	S_1		1/1	19	19.0	0	19+	0	0	0	0	0
	half-sib	12	69/65	18-21	11.0	9	18.3	9	39	26	6	870
21	S_1		4/3	19	13.5	5	19.0	1	2	1	1	250
	half-sib	4	45/43	18-21	11.3	10	17.3	9	40	31	15	4830
22	S_1		4/3	21	15.5	5	21+	0	2	0	1	0
	half-sib	8	103/105	18,19,21	11.6	12	17.1	11	78	70	12	2400
24	S_1		2/2	18	11.5	4	18+	0	2	0	1	0
	half-sib	1	4/4	18&21	12.0	4	14.3	5	2	3	26	2640
25	S_1		7/6	19	10.5	9	19.0	1	6	1	9	30
	half-sib	8	42/41	18-21	11.3	8	15.9	8	33	21	14	1045
30	S_1		2/2	19&21	12.0	2	20+	0	1	0	1	0
	half-sib	4	19/17	18&21	9.8	5	16.4	3	13	5	11	230
37	S_1		3/0									
	half-sib	[7]5	23/23	18&21								
39	S_1		1/1	21	10.0	7	18.0	1	1	1	13	105
	half-sib	[7]5	15/14	18&21	10.6	3	18.7	3	7	5	4	390
45	S_1		2/0									
	half-sib	2	7/7	18&21								
54	S_1		6/2	20	12.0	1	20+	0	1	0	1	0
	half-sib	12	54/48	18-20	11.2	5	16.9	5	18	8	1	185
58	S_1		18/18	21	13.1	12	18.7	6	15	10	7	745
	half-sib	19	182/163	18,20,21	11.4	13	17.0	9	114	86	10	3115
59	S_1		3/1	19	14.0	2	16.0	4	1	1	0	2200
	half-sib	3	17/14	19&20	11.2	2	17.8	5	8	8	6	3480
61	S_1		3/1	18	13.0	3			1			
	half-sib	[7]2	7/6	18	9.0	2			1			
63	S_1		7/6	20	15.6	6	20.0	1	5	1	0	3
	half-sib	6	54/48	18-20	11.3	8	17.9	8	27	22	4	1305
65	S_1		5/4	18	12.0	3	18+	0	4	0		0
	half-sib	3	19/17	18-19	10.5	2	15.5	2	3	4		665
69	S_1		10/6	19	14.0	8	13.0	2	5	1	0	1
	half-sib	4	10/10	19	10.5	4	19.0	1	3	1	4	2
70	S_1		1/0									
	half-sib	[7]4	17/17	18&19								
Totals[8]	S_1		109/72	348	246.2	85	338.2+	21	61/72	18/72	36	3920
	half-sib	158	1096/1014	347	195.1	121	305.8	106	604/946	446/946	137	25427
Pairs			22	18	18	18	17	17	18	17	16	17
			Percent survival									
Means	S_1		66.0	19.3	13.7	4.7	19.9	1.2	84.7%	25.0%	2.2	230.6
	half-sib		92.5	19.3	10.8	6.7	18.0	6.2	63.8%	47.1%	8.6	1495.7
Mean difference			-26.5%**	0.0	+2.9**	-2.0*	+1.9*	-5.0**	+20.9%**	-22.1%*	-6.4**	-1265.1 **

[1] S_1's are trees of the first selfed generation from the specified mother trees; half-sibs are either control-pollinated, full-sib trees or wind-pollinated "half-sib" trees of the same mother tree, from a given number of different sib lines; all are half-sibs of the S_1 trees.

[2] Planted trees excluded those dying from blister rust before fruiting; surviving trees include those alive in 1972, plus those fruiting prior to death.

[3] Except on trees being bred for special purposes (S_1's, a few full-sibs, etc.), arboretum-wide observations on female fruiting were discontinued once it became general (after 1966). Observations on male fruiting, however, are complete through 1972. Thus total female strobili per average tree are compared only through 1966, total male strobili through 1972.

[4] The five developmental stages correspond to (1) buds small to large (scales not open, prior to or at time of pollination bagging), (2) maximum receptivity (pollination time), (3) strobilus scales closed (time of pollination bag removal), (4) strobili persistent to second year (time of cone insect bagging), and (5) mature cones (time of cone collection).

[5] The + symbol indicates that the S_1 or sib lines had not produced strobili through 1972. For purposes of comparing pairs of values, these lines were treated as though they all produced strobili in 1973 (i.e., 18+ = 19, 19+ = 20, etc.).

[6] Dashes in blank cell indicate that phenomenon occurred but was not observed.

Table 3.--*(Con.)*

Parent (mother) tree number (1)	Controlled crosses: Attempted (14)	Controlled crosses: Yielding mature cones (15)	Live female strobili at five successive developmental stages[4]: Bud stage, May 1st yr. (16)	Pollen receptive stage, June 1st yr. (17)	Scales closed stage, July 1st yr. (18)	Overwintered conelet stage May 2nd yr. (19)	Mature cone stage, Sept. 2nd yr. (20)	Loss--buds to mature cones (21)	Crosses yielding filled seed (22)	Seed production & weight: Avg. filled seeds per cone (23)	Avg. hollow seeds per cone (24)	Avg. filled seed weight (25)
								Percent				Mg.
1	3	1	19	10	4	1	1	94.7	0	0.0	15.0	
	4	4	7	7	6	6	6	14.3	4	52.8	46.4	16.8
15	1	1	1	1	1	1	1	0.0	1	3.0	3.0	18.3
	16	10	89	83	[6]--	--	51	42.7	10	52.9	43.1	16.3
17	7	2	87	49	43	7	5	94.3	2	6.6	24.0	21.2
	44	39	196	177	162	148	145	23.0	39	55.5	29.1	20.1
18												
19	23	6	153	63	32	20	12	92.2	0	0.0	30.7	
	186	151	1686	1498	--	--	992	41.2	150	42.8	40.8	18.5
20												
21	5	4	61	57	34	17	13	78.7	4	2.9	11.0	13.1
	39	35	316	293	257	216	207	34.5	35	44.4	34.9	18.5
22	4	1	6	6	5	2	1	83.3	1	3.0	20.0	14.0
	117	100	1387	1307	--	--	830	40.2	91	54.3	27.6	18.6
24	5	1	11	9	9	3	1	90.9	0	0.0	3.0	
	2	2	20	18	16	15	14	30.0	2	58.4	15.8	18.3
25	27	18	177	153	77	45	42	76.3	17	33.7	43.1	18.1
	37	23	221	206	140	106	98	55.6	23	37.3	35.4	15.9
30	2	0	10	1	0	0	0	100.0	0			
	20	9	97	94	65	45	37	66.4	8	42.5	39.4	16.7
37												
39	7	5	74	60	26	16	14	81.1	5	28.4	42.0	14.8
	7	5	38	37	26	24	21	44.8	5	89.8	23.4	18.9
45												
54	1	1	5	3	2	2	2	60.0	1	1.0	40.0	13.0
	9	6	31	26	22	21	21	32.3	6	28.7	33.6	15.6
58	52	41	557	418	255	183	171	69.3	34	6.5	23.3	13.4
	127	100	973	871	--	--	667	31.4	98	57.9	30.6	20.1
59	2	2	13	12	6	5	5	61.5	1	28.5	35.8	14.6
	4	4	20	18	12	10	8	60.0	4	41.4	26.5	14.0
61	3	0	5	1	1	0	0	100.0				
	10	8	1	1	1	1	1	0.0	1	5.0	54.0	4.8
63	8	7	57	52	46	27	24	57.9	6	14.2	37.4	13.8
	15	11	59	56	44	39	37	37.3	11	22.5	39.5	16.4
65	7	3	14	14	4	3	3	78.6	3	18.7	35.3	11.5
	1	1	12	12	12	12	12	0.0	1	48.2	18.1	18.7
69	12	5	107	32	13	8	4	96.3	4	3.1	18.6	14.6
	4	2	20	17	--	--	9	55.0	2	15.2	50.6	11.1
70												
Totals	169	98	1357	941	252/533	126/533	299/1357	1315.1	79	149.6	382.2	180.4
	642	510	5173	4721	763/1018	643/1018	3156/5173	608.7	489	702.1	495.4	204.2
Pairs	17	17	17	17	12	12	17	17	16	15	15	12
			Periodic percent losses[9]									
Means		58.0%	0.0	31.2	27.2	21.1	3.0	78.0	46.7%	10.0	25.5	15.0
		79.4%	0.0	5.9	16.3	7.2	3.6	39.0	76.2%	46.8	33.0	17.0
Mean difference		-21.4%*		+25.3*	+10.9*	+13.9	-0.6	+39.0**	-29.5%*	-36.8**	-7.5	-2.0

[7]All 22 of the groups of half-sib lines except those with the footnote contain one wind-pollinated line.

[8]In some columns, the base number with which the column total should be compared is given following a slash (column 10, 11, 18-20). This base number may be reduced from the number given in a preceding applicable column (e.g., 946 in columns 10 and 11 rather than 1014 from column 4). Reduction occurred because certain data pairs (S_1's vs. half-sibs of the same mother-tree line) were not comparable--all S_1's died before producing strobili (lines 18, 37, 45, and 70), neither S_1's nor half-sibs bore male strobili (line 61), or when total number of strobili per tree was less than 1 (lines 61 and 65). Incomplete observations in some half-sib lines also reduced the number of data pairs (column 18, 19).

[9]For five of the 17 half-sib data pairs observations were missing on closed and overwintered conelets. Consequently only 12 data pairs could be used to compute periodic percent losses and the differences in losses between S_1 and half-sib lines. For the 12 data pairs, S_1 strobilus loss (sum of periodic losses) totals 82.5 percent, vs. 78.0 percent for the 17 pairs. Half-sib strobilus loss totals 33.0 percent, vs. 39.0 percent for the 17 pairs.

*Mean of difference significant at 5 percent level of probability, paired "t" test.

**Mean of difference significant at 1 percent level. Where differences are expressed in percent, the analysis was made using percents transformed into angles = arcsin $\sqrt{\text{percent}}$.

Crossing Success as Measured by Production of Mature Female Cones and Filled Seeds on S_1's

On S_1's, as compared with outcrosses, about 20 percent fewer of the second-generation inbred crosses attempted resulted in production of mature cones, 30 percent fewer resulted in production of filled seeds, and less than one-fourth as many filled seeds per cone were produced (table 3). Losses of female strobili on S_1 trees, between the unopened bud stage and mature cone stage, are twice as great (78 vs. 39 percent) as on the related, outcrossed trees (table 3). Almost two-thirds of this attrition in female strobili (58 of 78 percent) occurs the first year--either before or shortly after the scales open and the strobili are pollinated (31 percent), or before "setting" of the strobilus at the time of scale swelling and strobilus closure (27 percent). Apparently, these losses are not due to pollination failures, but reflect the reduced ability of the S_1 mother trees to support and mature normal strobili. Again, the effect seems to be least pronounced in the S_1's from comparatively self-fertile mother trees (25 and 58, vs. 19).

Once mature cones are borne, filled seed yield may be nil (6 crosses of S_1's of mother tree 19), low but consistent (41 crosses of S_1's of tree 58), or even consistently good (18 crosses of S_1's of tree 25). The average yield from mature cones produced in 79 crosses made on S_1 trees of 15 different lines was 10.0 filled seed per cone.

In table 3, the crosses of S_1's parents are considered only as a group--they are not classified as S_2's, S_1 X full-sib, etc. In table 4, however, crossing success, attrition of female strobili, and mature cone and seed yields are considered according to type of cross. Besides data for the second-generation inbred crosses, table 4 also provides data for a base outcross population as well as for various types of first-generation inbred crosses (half-sib, full-sib, backcross, and S_1 matings). Types of matings are arranged in order of increasing inbreeding coefficient.

All types of first- and second-generation inbred matings produced some mature cones and filled seeds (table 4). In general, where there is a base of more than a few attempted crosses, at higher levels of inbreeding fewer of the crosses produced mature cones, and filled seed yields were lower. The majority of cones from second-generation inbred matings that reach maturity contain filled seeds, however. There is little failure late in the reproductive process.

Table 4.--*Cone and seed yields in relation to level of inbreeding in crosses of western white pine trees*

Type of cross	Inbreeding coefficient (F)	Crosses attempted	Live female strobili at successive developmental stages: Bud	Pollen receptive	Scales closed	Over-wintered conelet	Mature cone	Loss, buds to: mature cones	Crosses yielding mature cones		Crosses yielding filled seed		Seeds per cone, average: Filled	Hollow
								Percent		*Percent*		*Percent*		
Population outcross	[1]0.000+	642	5173	4721	--	--	3156	35.8	510	79.4	489	76.2	46.8	33.0
S_1 outcross	0.000	4	7	7	--	--	4	42.8	1	14.3	1	14.3	[2]64.7	16.8
S_1 single cross	0.000	67	519	413	223	116	98	81.1	32	47.8	30	44.8	16.9	23.9
Half-sib cross	0.125	35	337	264	208	182	169	49.9	29	82.8	28	80.0	40.0	26.6
Full-sib cross	0.250	87	836	712	596	496	448	46.4	65	74.7	61	69.0	30.8	34.3
Backcross	0.250	134	690	612	588	467	443	35.8	108	80.6	107	79.1	39.9	43.4
S_1 X half-sib	0.250	3	30	30	17	11	10	66.7	2	66.7	2	66.7	15.6	18.6
S_1 cross	0.500	46	459	4437	341	275	266	42.0	38	82.6	37	80.4	30.1	54.9
S_1 backcross	0.500	60	345	302	231	135	105	69.6	36	60.0	28	45.0	12.3	40.4
S_1 X full-sib	0.500	22	250	158	116	71	64	74.4	16	72.7	11	50.0	6.2	26.7
S_2 cross	0.750	9	111	92	67	36	35	68.5	7	77.8	6	66.7	2.5	20.1

[1]Degree of inbreeding in natural populations is unknown, but the coefficient probably exceeds zero.
[2]Yield from four cones of one cross with an exceptionally self-fertile parent (No. 25).

DISCUSSION AND CONCLUSIONS

The feasibility and efficiency of an inbreeding program depend upon five conditions:

Survival of inbred plants to fruiting age

Fruiting within a reasonable time, and by a reasonable proportion of the plants

Success of the inbred pollinations, or attainment of useful levels of filled seed production

Germination, survival, and fruiting of successive generations of inbred seed and seedlings

Restoration of reproductive vigor (seed bearing) when inbreds are finally outcrossed

The record on the first four of these conditions is reasonably complete for first- and second-generation inbreds of three of the species covered in the literature review (Norway spruce, Douglas-fir, and Japanese black pine), and it is here extended to western white pine. The record of success and levels of seed production attained in second-generation crossing of these four conifers is reviewed in table 5.

Where the number of second-generation crosses attempted in these four conifers has been adequate, generally there is fair crossing success. From 45 to 100 percent of the crosses produced mature cones, and 25 to 100 percent produced filled seeds.

Filled seed yields per cone have been low in S_2, S_1 X full-sib, and S_1 backcrosses; fair in S_1 single crosses. Data on germination of second-generation inbreds are scanty, and cover only three of the four species of table 5--*Pinus monticola* only for seed from S_1 backcrosses, and *Picea abies* only for seed from S_2 crosses. Nevertheless, in six tests (41 to 1,821 seed per test), the second-generation inbred seed has germinated well--in the 40 to 80 percent range. For *Pinus monticola*, S_1 seed germinated at the 50 percent level (Bingham and Squillace 1955) and there has been no further dropoff in germination of S_1 backcross seed. This confirms Andersson's (1965) observations that reduction in germination occurred principally in the S_1 seed.

Similarly, survival of second-generation inbreds of Douglas-fir and western white pine appears to be good. Orr-Ewing (1965) showed that first-year survival in those second-generation inbred seed lots having more than 10 seed ranged from 30 to 90 percent, and averaged 65 percent. Between 45 and 80 percent (average 57 percent) of the seedlings in five western white pine S_1 backcross seed lots having more than 10 seed survived 3 years in the nursery. Many of them are now 7 to 8 years old in the field.

Righter (1962), and of course many maize breeders before him, have recognized the "reproductive weakness" of inbred maternal parents. He states that "seed yield per

Table 5.--*Female strobilus yield, seed yields, and seed germination following crossing of* S_1 *trees in* Pinaceae

Type of cross	Species	Crosses attempted	Parental S_1 trees crossed	Original parents of S_1's	Crosses yielding filled seeds		Crosses yielding mature cones		Strobilus loss, pollination to cone collection	Average seed per cone		Filled seed		
										Filled	Hollow	Total	Crosses	Germination
						Percent		*Percent*	*Percent*					*Percent*
S_2	*Picea abies*[1]	5	5	2	3	60.0	4	80.0	--	1.2	205.4	41	3	79.2
	Pseudotsuga menziesii[2]	30	23	4	27	90.0	30	100.0	16.5	1.6	40.6	95	8	42.8
	Pinus thunbergiana[3]	7	[4]7-	3	3	42.8	4	57.1	87.0	5.8	6.1	--	--	--
	Pinus monticola	9	7	4	6	66.7	7	77.8	68.5	2.5	20.1	--	--	--
S_1 X full-sib	*Pseudotsuga menziesii*	2	4	2	2	100.0	2	100.0	[5]33.3	24.4	33.2	171	2	73.3
	Pinus thunbergiana	20	35-	3	10	50.0	10	50.0	84.0	7.4	6.6	--	--	--
	Pinus monticola	22	11	4	11	50.0	16	72.7	74.4	6.2	26.7	--	--	--
S_1 back-cross	*Pseudotsuga menziesii*	15	15	3	15	100.0	15	100.0	[5]59.8	6.8	36.0	476	15	58.0
	Pinus thunbergiana	20	20-	3	5	25.0	9	45.0	85.2	5.1	3.3	--	--	--
	Pinus monticola	60	44	14	28	45.0	36	60.0	69.6	12.3	40.4	307	6	51.4
Single cross	*Pseudotsuga menziesii*	25	25	7	24	96.0	25	100.0	[5]30.0	18.2	24.0	1821	23	57.5
	Pinus thunbergiana	5	5+	3+	0	0.0	1	20.0	91.7					
	Pinus monticola	67	41	14	30	44.8	32	47.8	81.1	16.9	23.9	--	--	--

[1]After Andersson (1965).
[2]After Orr-Ewing (1965 and 1969), amended by Orr-Ewing (personal communication, 1973).
[3]After Katsuta (1966).
[4]Cited publications are unclear as to exact numbers, but they are some what less (-) or more (+) than numbers having these signs.
[5]Based on 1962 pollinations only, using a type of pollination bag that may have increased losses (Orr-Ewing, personal communication, 1973).

plant is too low for practical purposes," and explains how reproductive vigor is restored in plants from single and double crossing of two or four inbred lines. Actually the maize breeders also selected among their inbred lines for reproductive vigor, and the same principle can be applied to western white pine and other conifers.

An example of the effect of thus selecting for comparatively high self-fertility can be drawn from our results with western white pine. If we had continued the inbreeding program using only those highly self-fertile parents that yielded 60 or more filled S_1 seed per cone (Bingham and Squillace 1955, table 1), we would have selected seven of the nine S_1 lines in which second-generation inbreeding gave low to fair, but consistent yields of filled S_2 seed (3 to 34 per cone).

The effectiveness of such selection for reproductive vigor is emphasized when, as in table 6, a comparison of second-generation cone and seed yields is made between S_1 trees from a comparatively self-sterile parent (tree 19) and those from comparatively self-fertile parents (trees 25 and 58).

Snyder (1968) shows that in Mississippi slash pine yield of filled seed per cone and germination of S_1 seeds are lower than in most other pines. He also shows (1968 and 1972) that inbreeding depression--measured in height growth reduction--increases in slash pine S_1 trees between the first and fifth years of growth (cf. also Bingham and Squillace 1955, and Barnes 1964, for the same phenomenon, ages 1 to 12 years, observed in western white pine). Nevertheless, Snyder's cones from "self-compatible" parents yielded 2 to 13 filled seed per cone compared to 30+ seed per wind-pollinated cone, and one-third or more of the S_1 seeds germinated.

Snyder (1968) concluded, from the low filled-seed and seedling yields per 100 self-pollinated strobili, from the probable (but unknown) delay in flowering of the S_1 trees, and from apparent indications of a relatively low level of nonadditive variance in most traits of southern pines, that an inbreeding program was neither feasible nor practical for improving most characters of slash pine. His own evidence for the first inbred slash pine generation, however, coupled with evidence from second-generation crossing in four other species in *Pinaceae*, makes these conclusions seem premature. The arguments of Franklin (1969) against inbreeding for improvement of loblolly pine (*Pinus taeda* L.) are much stronger, including unknown effects of probably greater pregerminative selection in inbreds, hypersensitivity of inbreds to environmental stress, the relative difficulty (thus high cost) of maintaining inbreds, and the present disaffection of even the maize breeders with the traditional inbreeding-outcrossing hybrid method.

Despite these problems, continuation of *experimental* inbreeding programs in some conifers seems warranted. Consistent, if small, S_1 and S_2 seed yields, and S_1 plants that fruit within reasonable periods, have been obtained in at least four conifers. Also, experimental efficiency probably could be greatly enhanced through selection of comparatively self-fertile parents for subsequent cycles of inbreeding.

Questions that remain for the inbreeder center on long-term economic and genetic practicability, and on the stability of gains under inbreeding as opposed to outcross breeding. To answer these questions, we need to proceed on an experimental basis toward answering such subordinate questions as: What is the gain from one generation of inbreeding followed immediately by single crossing of selected, vigorous S_1's? and, Is reproductive vigor of the inbreds restored in these early single-cross lines, so that the double crosses may be produced quickly, economically, and in quantity?

It would seem that gains anywhere near those achieved in maize double crossing would finance such an abbreviated inbreeding program in trees. If growth of single-cross lines from S_1 crossing represents little or no gain from heterosis, and bears no relation to vigor of parental S_1 lines, then it will be time to reconsider the practicality of inbreeding programs in forest trees.

Table 6.--*Cone and seed yields following crossings on S_1 trees from comparatively self-sterile and self-fertile parents, western white pine*

Original parent number	Crossing success					
	S_2's	S_1 full-sibs	S_1 back-crosses	Single crosses	Half-sib out-crosses	Total
			CROSSES ATTEMPTED			
19	1	1	10	9	2	23
25	--	--	11	14	2	27
58	6	19	17	9	1	52
			CROSSES YIELDING MATURE CONES			
19	0	0	5	1	0	6
25	--	--	7	9	2	18
58	6	16	11	8	0	41
			CROSSES YIELDING FILLED SEED			
19	--	--	0	0	--	0
25	--	--	6	9	2	17
58	5	11	11	7	--	34
			FILLED SEED PER CONE, AVERAGE			
19	--	--	0.0	0.0	--	
25	--	--	34.4	37.3	32.5	
58	3.3	9.1	10.1	5.3	--	

SUMMARY

There are no reproductive barriers in western white pine restrictive enough to preclude an inbreeding program. Filled seed yields following second-generation inbreeding are low, but consistent, from a variety of matings. Efficiency of the program can be increased by proceeding only with S_1 lines where S_1 seed yield is relatively high.

Reproductive maturity of western white pine S_1 lines was attained at about 15 to 20 years of age, and the fruiting of S_2 lines may be delayed even more. Meanwhile, because of the length of inbred generations, and because the greatest increment of the increase of homozygosity occurs in the first inbred generation, it seems expedient to begin single crossing among the better S_1 lines immediately. Some success has accompanied similar "early" crossing in maize (cf. Lonnquist and Williams 1967). Performance of these single-cross progenies, and the level to which their reproductive vigor is restored, will be critical information in the decision as to whether we should embark on a practical inbreeding program in western white pine.

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BINGHAM, RICHARD T.
1973. Possibilities for improvement of western white pine by inbreeding. USDA For. Serv. Res. Pap. INT-144, 18 p., illus. (Intermountain Forest & Range Exp. Station, Ogden, Utah 84401.)

Pinus monticola S_1 seedling mortality, timing and extent of fruiting, strobilus attrition, crossing success, seed yield, and seed weight are compared for 18 S_1 lines and their outcrossed half-sib lines. No reproductive barriers are restrictive enough to preclude continued inbreeding. Filled seed yields from second generation inbreeding are low but consistent and large enough to justify continuing an experimental program. Results of experimental single crossing between S_1 lines should guide decision on a practical inbreeding program.

OXFORD: 165.413 : 174.7 : 181.521 : 181.522. KEYWORDS: Inbreeding, *Pinus monticola* (coniferae), cone initiation, seed production.

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Headquarters for the Intermountain Forest and Range Experiment Station are in Ogden, Utah. Field Research Work Units are maintained in:

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